Chapter 2
Biology

Key Questions:
   a) *What are the defining biological characteristics of O. mykiss?*
   b) *What are the habitat, harvest, and hatchery management implications of these biological characteristics?*
   c) *What management complexities result from these biological characteristics?*

2.1 Introduction

Steelhead are considered by many fisheries biologists to be the most difficult Pacific salmonid species to protect and manage because of the diversity in life history patterns that exist both within and between populations. This diversity includes multiple times for the return of adults to natal streams, varying periods of freshwater and ocean residency, and plasticity of life history between generations. The life history of steelhead also differs from many *Oncorhynchus* species in several fundamental ways. These include the frequent presence of resident forms of *O. mykiss* and iteroparity, or the ability to complete more than one cycle of spawning. This diversity introduces management complexity – but also enables the species to persist in highly variable environments.

> *"The steelhead are a paradox and only their return is viewed with absolute certainty. They are composed of exceptions—every "fact" about their upstream migration will almost contain an opposite number somewhere else."*
>
> *Trey Combs, The Steelhead Trout*

Given the diversity of steelhead, our intent in this chapter is not to provide a comprehensive, population by population review of the biological characteristics of steelhead. Rather, we illustrate the diversity of steelhead throughout Washington, assess the habitat, harvest, and hatchery management implications of this diversity, and discuss the resulting the management complexities. More detailed presentations of the biological characteristics of steelhead can be found in Burgner et al. (1992), Busby et al (1996), Reiser et al. (1979), and Withler (1966).

2.2 Diversity Groups

Two genetically distinct groups of *O. mykiss* inhabit Washington (Allendorf 1975; Phelps et al. 1997), a coastal form native to the area west of the Cascade crest, and an inland form native to the area east of the Cascades. Both the coastal and inland forms exhibit anadromous and resident life histories. Behnke (1992) considers these two groups different subspecies, *O. mykiss irideus* and *O. mykiss gairdneri*, respectively. Inland *O. mykiss* are commonly referred to as redband trout, and in Washington the term can be used to describe any native resident or anadromous *O. mykiss* population east of the Cascades crest. This term needs to be used cautiously, however. Redband trout occur in British Columbia and in several western states. Wherever they occur, they are distinctive from the coastal form, but they do not consist of a single taxonomic entity (Behnke 1992; Currens 1997). Although they may seem morphologically and ecologically similar, a redband trout from Washington is genetically quite different from one from California.

Photo 2-1. Redband trout from the Naches River, March 2004. Photo source: Jim Cummins, WDFW.

Genetic, morphological, and life history variations and similarities exist among steelhead populations of Washington at finer geographic scales. Leider et al. (1994) identified seven Genetic Conservation Management Units (later called Genetic Diversity Units or GDUs) for steelhead in Washington. These were refined in subsequent analyses (Leider et al. 1995; Phelps et al. 1997) and eventually led to the identification of Evolutionarily Significant Units (ESUs) by NOAA Fisheries (Busby et al. 1996). While a GDU is strictly a biological method for organizing the diversity of steelhead, an ESU has regulatory implications under the Endangered Species Act. An ESU is a population or group of populations within a species that: 1) is substantially reproductively isolated from other populations (or groups of populations) of the same species and; 2) represents and important evolutionary legacy of the species as a whole (Waples 1991). NOAA Fisheries has identified 7 ESUs residing wholly or partially in Washington: 1) Puget Sound; 2) Olympic Peninsula; 3) Southwest Washington; 4) Lower Columbia River; 5) Middle Columbia River; 6) Upper Columbia River; and 7) Snake River Basin. ESUs and populations of steelhead in Washington are discussed further in Chapter 5, Population Structure.

2.3 Anadromous and Resident Life History Types

O. mykiss is a highly polymorphic species and Washington watersheds can be inhabited by resident (rainbow or redband trout), anadromous (steelhead), or a mixture of both life history types. Although anadromy appears to have some genetic basis (Thrower et al. 2004), it is a relatively complicated phenotype in this species as evidenced by its variability and plasticity of expression. The presence of alternative life history types can occur under a variety of conditions and, as the RSRP (2004) noted, "represents different phenomena in different locations, from a polymorphism within some populations to a secondary contact between divergent subpopulations to reproductively isolated, long-separated lineages".

Non-anadromous *O. mykiss*, referred to as rainbow trout, and which spend their entire life-cycle in freshwater, occur throughout the range of steelhead in the Pacific Northwest, and in areas that are not accessible to steelhead due to geomorphology or human intervention. There is genetic support for the hypothesis that resident life-history forms of *O. mykiss* developed from the anadromous form because greater genetic similarity often occurs between the two forms within a basin instead of between the same life-history types in different basins (Phelps et al. 1994; Phelps et al. 1997; Docker and Heath 2003).

Resident rainbow trout populations often occur in smaller streams where large anadromous adults cannot migrate, but these trout will also use mainstem areas of larger rivers during their life cycle. There are few locations in the state where the abundance of sympatric resident and anadromous steelhead is estimated. Resident trout may have been more abundant in lower mainstem areas of large rivers in the past, but have vanished due to habitat alteration and fishing pressure (Kostow 2003). Resident trout also inhabit lake systems, which are not always strictly land-locked, as small fish may be able to move downstream into steelhead-accessible areas.

Hatchery-produced rainbow trout that are planted in lakes throughout Washington are nearly all non-native origin, having been derived from trout lineages of California (Crawford 1979). It is assumed that they behave as resident, non-migratory trout, although studies in Snow Creek suggest that at least some will enter marine waters where downstream passage is possible (Michael 1989). If spawning occurred among hatchery-origin trout it is also assumed that, as a result of their ancestry and domestication history, they would rarely, if ever, produce anadromous offspring.

2.3.1 Evolution of Anadromy

Gross (1987) theorized that diadromy would evolve if the fitness (W) costs of migration were less than the benefits associated with rearing in an alternative environment. Applying this theory to *O. mykiss*, we would expect that anadromy would evolve if the costs of smolt and adult migration were less than the survival and reproductive benefits resulting from rearing in marine waters:

$$W(H_1)_A + W(H_2)_A + W(M_T)_A > W(H_1)_R$$

where $W(H_1)_A$ is the growth and survival of anadromous fish in freshwater; $W(H_2)_A$ is the growth and survival of anadromous fish in marine waters; $W(H_1)_A$ is the growth and survival of anadromous fish during the smolt and adult migration ; and $W(H_1)_R$ is the fitness of resident fish (by definition set equal to 1).

In an extensive review of anadromy in salmonds, Hendry et al. (2004) predicted that "The tendency for anadromy should decrease as its benefits decrease, with the same true for non-anadromy. The relative benefits of anadromy, and therefore its prevalence, should decrease with increasing freshwater productivity (growth) or increasing migratory difficulty (distance or elevation)." This prediction, if correct, has important ramifications for evaluating the potential effects of harvest, habitat, hatchery management actions assessing the status of populations of *O. mykiss*.

Fishery management actions that disproportionately affect the mortality of the resident or anadromous fish may shift the relative abundance of these life history types. Hendry et al. (2004) reviewed studies of Russian lakes where fishery mortality has resulted in a reduction in the abundance of anadromous adult sockeye salmon. Concurrently, these studies found "a decrease in juvenile densities, an increase in juvenile growth, and a dramatic increase in the proportion of residuals among males (13% to 82% in Uyeginsk; 26% to 92% in Sal'nee)" (Hendry et al. 2004).

Habitat characteristics can differentially affect the reproductive potential and relative abundance of the resident and anadromous life history types. Bohlin et al. (2001) evaluated the density of resident and anadromous juvenile brown trout in populations in streams along the coast of Sweden. The altitude of the stream in which the population occurred was assumed to be a surrogate measure of the costs associated with migration to marine waters. At low elevations, both resident and anadromous populations existed, but the density of anadromous juveniles was greater than the abundance of resident juveniles. As the altitude increased the density of anadromous, but not resident, brown trout decreased. Anadromous and resident brown trout were of similar abundance at an altitude of approximately 150 meters, and few anadromous

populations existed above that elevation. Bohlin et al. interpreted these observations as support for the hypothesis that increased costs of migration to marine waters were associated with higher altitude, and that higher costs of migration were associated with a reduced likelihood of anadromy.

2.3.2 Reproductive Interactions

In drainages where anadromous fish have access, reproductive interactions may occur between steelhead and resident rainbow trout. Researchers are beginning to document interbreeding and population relationships or structuring between resident and anadromous *O. mykiss* within a watershed. Zimmerman and Reeves (2000) used otolith microchemistry and spawning ground surveys to determine whether steelhead had resident fish maternal origins and whether resident trout had anadromous fish maternal origins. They found that resident and anadromous *O. mykiss* in Deschutes River, Oregon had a high probability of being reproductively isolated populations, whereas in a coastal Canadian drainage (Babine River) complete reproductive isolation was not likely the case. Pearsons et al. (in press) evaluated the potential for gene flow between Yakima Basin resident and anadromous *O. mykiss* using ecological and genetic data. They observed many instances of interbreeding between rainbow trout and steelhead and in one drainage, the North Fork Teanaway River, found that wild rainbow trout and steelhead were genetically indistinguishable. In a study of genetic relatedness among offspring from steelhead redds in the Hamma Hamma River, Kuligowski et al. (2005) found a male-biased sex ratio (16 males to at least 5 females) among parents that they attributed to matings by either a male resident trout or precocial steelhead parr with female steelhead.

In a Hood River, Oregon steelhead reproductive success study using DNA pedigree analysis methods, researchers estimated that about 40% of returning steelhead had non-anadromous male parents (Ardren 2003; Blouin 2003). It is not known which type of non-anadromous (resident trout, planted hatchery trout, or residualized steelhead) male parent were the contributors, but work to determine this is underway. A pedigree-based study in Snow Creek (Olympic Peninsula, Washington) showed that in some years of low steelhead return mature (precocious) non-anadromous males may collectively be more successful at producing anadromous offspring than anadromous males (Seamons et al. 2004). In another Snow Creek study, Ardren and Kapuscinski (2003) found that the ratio of effective population size to the actual number of steelhead spawners was significantly higher in years with low steelhead spawner density. Seamons et al. (2004) stated that an explanation for this observed pattern may be a proportional increase in reproductive success of resident males when few anadromous males occur. These results suggest that resident males may increase the probability of persistence for a small steelhead population.

Photo 2-2. Spawning pairs of *O. mykiss* may include adults of anadromous, resident, or mixed origin. Resident males may be an important contributor to the viability of small populations. Photo source: unknown.

Given the results of these and other studies, there is much interest in determining the rate and extent that resident trout populations might produce steelhead. In an on-going breeding study using Grande Ronde Basin (OR) steelhead and trout, all possible crosses between resident trout and between trout and steelhead all produced out-migrating smolts, and the steelhead by steelhead crosses produced the largest proportion of detected outmigrants (Ruzycki et al. 2003). Adults from these crosses are beginning to return, and after all age groups return, the ability of Grande Ronde resident trout to produce steelhead will be determined. In a breeding study focused on heritabilities of growth, precocious maturation and smolting using crosses among steelhead and lake-resident rainbow trout derived from steelhead 70 year earlier, Thrower et al. (2004) found that the lake population retained the ability to produce smolts, and that resident crosses produced lower proportions of smolts than steelhead crosses. The results of Thrower and Joyce (2004) indicated that marine survival of smolts of the lake-derived fish was poor relative to the smolts derived from anadromous parents.

Breeding also can occur between resident trout and residualized precocious male steelhead (Pearsons et al. in press), which are offspring of steelhead parents that have become mature while residing in freshwater. The importance of precocious male reproductive contributions, i.e. the proportion of offspring they produce within a steelhead population, is only beginning to be studied. As indicated by the steelhead

studies described above, however, this may be an important life history variation for steelhead. Males can reproduce without the survival risks of going to sea.

A few studies have documented reproduction between non-native hatchery rainbow trout and hatchery steelhead and between these hatchery trout and native resident *O. mykiss* (Campton and Johnston 1985; Pearsons et al. in press). However, the genetic impact of non-native hatchery trout stocking on resident native *O. mykiss* populations or steelhead populations often has been found to be less than expected given an extensive history of stocking. Kostow (2003) describes findings of this nature for a variety of Columbia Basin drainages.

Current information demonstrates that native, resident populations of *O. mykiss* are often a component of the genetic population structure of steelhead. This is likely to be particularly true among Columbia Basin inland steelhead because environments there often support large resident rainbow trout populations that are sympatric with steelhead. In coastal drainages, trout are often more abundant above artificial barriers such as dams than in drainages below them, which are usually dominated by steelhead. The resident life-history strategy may be favored under certain environmental conditions, and when migratory or ocean conditions are unfavorable for steelhead, resident fish may serve to maintain the genetic heritage of a drainage's *O. mykiss* population. Native, resident trout populations increase the genetic diversity of the species, which likely provides for a greater ability to adapt to a wider range of environmental conditions.

The potential for reproductive interaction of the resident and anadromous life history forms indicate that effective management may require, at least in some watersheds, consideration of steelhead parr, smolts, and rainbow trout as integral components of the *O. mykiss* population.

2.3.3 Ecological Factors Affecting Anadromy

Construction of dams and other anthropogenic activities may have ecological effects that alter the prevalence of anadromy. Morita et al. (2000) found that juveniles of white-spotted char located below dams were more likely to migrate to marine waters than white-spotted char located above the dams. However, juvenile char collected from both upstream and downstream of a dam were then transplanted to a barren location upstream of a dam in another stream. Low rates of smolting were observed regardless of whether the juveniles originated from the upstream (resident) or the downstream population (resident and anadromous). Morita et al. (2000) suggested that the reduction in anadromy observed upstream of dams was a phenotypic response to the reduced density and faster growth rate observed for char populations located upstream

of dams. The phenotypic plasticity expressed, the authors concluded, "can have an important role in preventing local extinction."

The projected benefits of habitat restoration projects to steelhead populations may vary depending upon model assumptions regarding interactions with rainbow trout. Preliminary analysis of rainbow trout and steelhead in the Yakima River (Mobrand-Jones & Stokes 2005) illustrate the potential importance of considering rainbow trout and steelhead interactions. Steelhead emigrating from or returning to the Yakima River must pass four dams on the Columbia River and up to seven diversion dams in the subbasin. Resident and anadromous population of *O. mykiss* exist in the subbasin, but rainbow trout are currently more abundant than steehead in the upper Yakima River. Mortality related to dam passage has been hypothesized to be a significant factor affecting the relative abundance of rainbow trout and steelhead. Based upon the work of Gross (1987), a model was developed to help guide the evaluation of potential restoration actions. In some cases, the predicted increases in steelhead abundance resulting from restoration actions were dependent on the inclusion or exclusion in the analysis of the existing populations of rainbow trout. For example, the abundance of steelhead in the West Fork Teanaway River was predicted to increase from 0 adults to 63 adults with the elimination of dam-related mortality in Yakima River and without consideration of rainbow trout (Watson pers. comm.). When rainbow trout were included in the analysis, the abundance of steelhead was predicted to increase from 0 adults to 12 adults (Mobrand-Jones & Stokes 2005).

2.3.4 Proximal Factors Affecting Anadromy

The size or growth rate of juvenile salmonids appears to be a significant factor regulating the initiation of smolt metamorphosis (Bohlin et al. 1993, 1996; Okland et al. 1993). Evidence for this relationship for steelhead includes a relatively consistent size (160 mm fork length) but variable age of migrants along the west coast of North America (Burgner 1992) and the development of osmoregulatory capability at a size of 140 to 160 mm (Conte and Wagner 1965).

Thorpe et al. (1998; see also Metcalfe 1998) developed a general theory for salmonid life histories that relates proximal factors, such as lipid reserves or length, to smolting and maturation. A key feature of the theory is that a series of developmental switches were hypothesized to regulate the initiation of the smolt metamorphosis and maturation. Metcalfe (1998) described the application of this theory to Atlantic salmon:

> "Therefore analyses of size at the time of spawning or entry to sea tell us nothing about the underlying triggering mechanisms, since size by this stage is partly a consequence, rather than a cause, of the life history strategy that has

been adopted. Models based on threshold size at this time (e.g., Power and Power 1994) do not therefore present a real picture of the life history decisions reached by the fish. We must instead examine the state of the fish at the time of the decision: what makes a fish begin the process of smolt transformation in late summer or maturation in late autumn? Current evidence (summarized by Thorpe et al. 1998) suggests that these events are triggered if the fish is on course to surpass a threshold state (cf. Roff 1996) by the time of entry to the sea or time of spawning, respectively. Thus smolt transformation is triggered in late summer if the fish is set to exceed a threshold level of resources by the following autumn. In either case, the future state of the fish is presumably estimated from a combination of its current state and the rate at which that state is currently changing at the time of the life history decision. Therefore, in late summer the fish would be, in effect, estimating (from its current size and growth rate) what its size should be at the time of the smolt migration the following spring; if its projected size was above the genetically determined threshold then smolting would be triggered, while if it fell below the fish would remain a parr in freshwater for a further year…"

Photo 2-3. A series of developmental switches have been hypothesized to control the initiation of smolt metamorphosis and maturation. Photo source: Todd Pearsons, WDFW.

Improved understanding of the relationship between environmental factors (e.g., water temperature, stream flow), physiological status (e.g., length, growth rate), and life history patterns of steelhead would be a powerful tool for developing and evaluating management actions. Mangel et al. (2004) have proposed the development of models linking the physiological status and life history patterns of steelhead in the Central Valley and in coastal streams of California. In assessing the continued decline of steelhead in those areas more than 40 years after the major period of dam construction, Mangel et al. (2004) surmised that "…major shifts in the environment can result in a high proportion of fish that have entered an inappropriate pathway. Our overall hypothesis is that water flow levels and the temporal pattern of water delivery have a major impact on growth opportunity an life history expression in age-0 steelhead, which will echo through the rest of their life history and populations dynamics. Alteration of water flow patterns potentially disrupts the natural adaptive responses of juvenile steelhead, resulting in reduced survival as fish make crucial mistakes in selected life history trajectories."

2.3.5 Ecological Interactions

For purposes of this discussion, ecological interactions are defined as any direct or indirect interactions that would occur between resident and anadromous *O. mykiss* other than interbreeding. Competition (for food and habitat) and predation are two major types of ecological interactions expected between the two life-history forms. In drainages where native resident and anadromous *O. mykiss* have occurred together over long time periods, it is reasonable to assume that the net outcome of interactions perpetuates the existence of both forms. In other words, resource use by one form does not lead to the decline of the other.

Photo 2-4. Scarring and ragged fins are sometimes evident after competitive attacks between juvenile *O. mykiss*. Little is known about the effects of competition between the juvenile anadromous and resident life history types. Photo source: Todd Pearsons, WDFW.

The greatest opportunity for competition between resident trout and steelhead occurs during the stream-rearing period for juvenile steelhead, which is quite variable in length. Juvenile resident trout and steelhead would compete for the same food resources and territories where and when they shared habitat. Although spatial distributions can overlap extensively, resident trout often inhabit smaller or higher elevation streams not utilized by adult steelhead (Pearsons et al. in press), and this

partitioning reduces competition. However, interactions between both types of juveniles are not limited to overlapping habitats of adults. Rearing steelhead may migrate into trout territories, and young trout may move downstream into steelhead habitat. Juvenile abundances are regulated by food and space resources, predation, flooding, drought, and many other factors (Keeley 2001). Competition is a consistent factor and changes in abundance of resident or steelhead progeny would likely modify competitive pressures on the alternative form.

Resident trout might be expected to prey on smaller juveniles of their species. Steelhead and sympatric trout have similar spawn timing, and even if no interbreeding occurred, their juveniles would likely be present and available as prey to adult trout at generally the same time. Thus, unless there is some behavioral difference between trout and steelhead juveniles that increases either's predation risk, it is likely that piscivorous resident trout (or juvenile steelhead) could prey equally on both juvenile types. At this time we have found no empirical studies documenting resident rainbow trout differential predation effects on steelhead. The issue of whether rainbow trout could pose a significant predation risk to steelhead is likely most relevant where habitat damage, fisheries, or artificial stocking has led to steelhead declines and enhanced trout abundance.

The discussion above is focused solely on native, naturally occurring steelhead and resident rainbow trout populations. Releases of hatchery-origin steelhead and trout can impose impacts on native populations through disease, competition, and predation. These types of ecological interactions have been studied extensively in the Yakima River Basin (Pearsons et al. 1994; Pearsons et al. 1996; McMichael et al. 1997; 1999a; 1999b; McMichael and Pearsons 2001). Artificial production programs and their potential effects on natural populations are discussed further in Chapter 3, Artificial Production.

2.4 Life History Diversity of Anadromous *O. mykiss*

2.4.1 Multiple Adult Run Times

Two broad life history types of steelhead exist in Washington: winter-run and summer-run fish. The life history types are principally distinguished by the timing of adult return and the level of sexual maturity at the time of river entry (Burgner et al. 1992). Adult winter steelhead typically return to the river mouth from November through May or early June, with peak spawning occurring from mid-April through mid-May in most Western Washington streams. Summer steelhead return to the river mouth between April and October, enter freshwater sexually immature, and require several months to mature and spawn. In general, summer steelhead spawn earlier in the year than winter steelhead.

Indigenous steelhead of both life history types exist in most large watersheds in western Washington. For example, sympatric populations of summer and winter steelhead exist in the Nooksack, Skagit, Stillaguamish, and Snohomish rivers in Puget Sound, and in the Quillayute, Hoh, Queets, and Quinault rivers on the Washington coast (see Chapter 5 for a more detailed discussion of population structure). In general, summer steelhead are not found in small watersheds in western Washington. Withler (1996) suggested that summer steelhead occurred in small, coastal watersheds of British Columbia only if seasonal migration barriers promoted the reproductive isolation and subsequent evolution of the summer and winter life history types. In contrast to western Washington, all historical steelhead populations in the interior Columbia River basin are of the summer life history type. A similar pattern in the distribution of steelhead is evident in British Columbia, where winter steelhead are absent from the interior Fraser River basin but predominate in coastal drainages (Withler 1966; Parkinson 1984).

The presence of summer and winter steelhead in the coastal rivers of British Columbia and Washington apparently resulted from the repeated evolution of run timing in multiple watersheds rather than the evolution of two run timing types with subsequent dispersal to multiple watersheds. Numerous studies have found that summer and winter steelhead from a particular coastal watershed are genetically more similar to one another than to populations with similar run timing in adjacent watersheds (Allendorf 1975; Utter and Allendorf 1977; Chilcote et al. 1980; Reisenbichler and Phelps 1989). Summer type steelhead in the interior Fraser and Columbia basins, however, are believed to have originated from two or more founding populations that existed in glacial refugia in the interior of these basins during the last glaciation (Beacham et al. 1999). The origin of summer and winter life history types has important implications for planning conservation efforts or evaluating hatchery programs (see Chapter 3, Artificial Production).

Research conducted at the Kalama River since 1974 provides a long-term assessment of the run timing of sympatric populations of summer and winter steelhead. Returning adults are collected at a trap (river km 17) located downstream of nearly all summer steelhead spawning areas (Crawford et al. 1977) and approximately 90% of the winter steelhead spawning areas (Hulett pers. comm.). The life history type of each fish passed upstream is determined by physical appearance and sexual maturity (Leider et al. 1984). The trapping data indicate that adult steelhead migrate upstream in every month of the year (Fig. 2-1). The peak passage of summer steelhead occurs on average in July, but adults return as early as April and as late as March the following year. Winter steelhead are migrating upstream at the trap site from October through July, with most of the adults generally passing upstream in April.
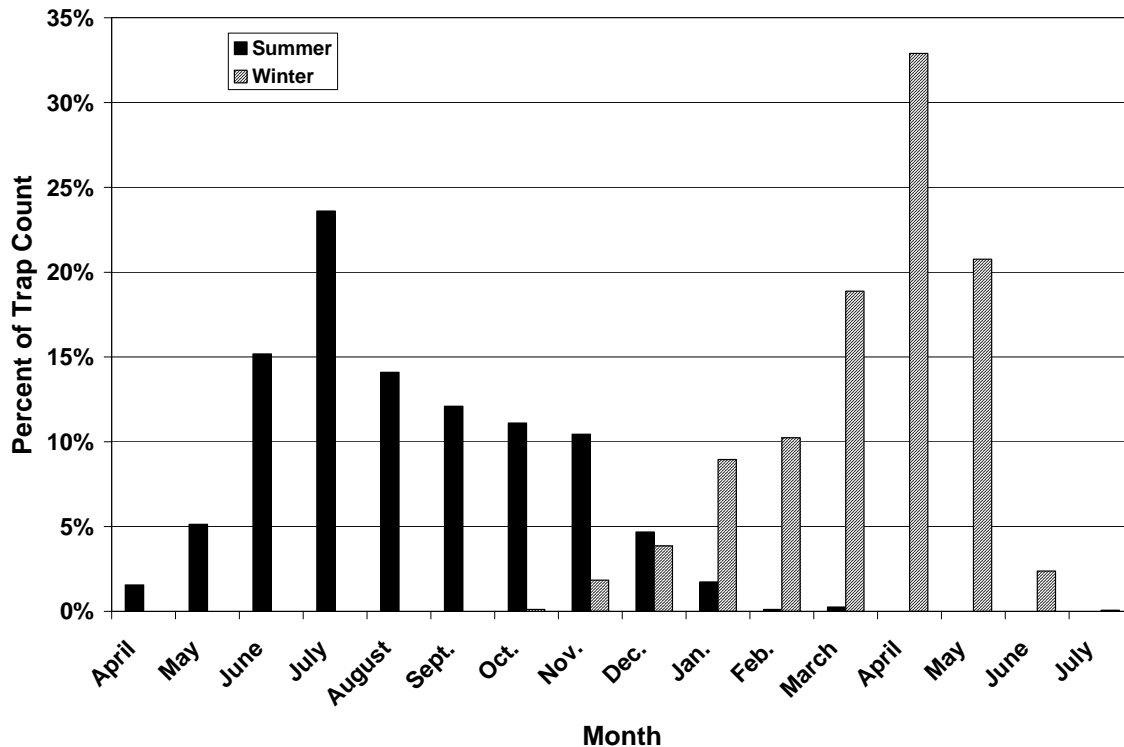
Figure 2-1. Average timing of natural-origin summer and winter steelhead past the Kalama River trap, 1976-1977 through 1995-1996 seasons.

The time period of spawning in the Kalama River is contracted relative to entry and migration past the trap. Leider et al. (1984) marked summer and winter steelhead prior to passing the fish upstream and subsequently monitored the date of spawning. In the three years of study, summer steelhead spawning occurred from December through April of the following year (Fig. 2-2). Peak spawning occurred in the month of February, 7 months months past the peak month of entry (July). Spawning of winter steelhead was observed from January through May, with most of the spawning occurring during the month of April (Fig. 2-3).

Estimates of spawn timing are available for only a limited number of other naturally-spawning populations of steelhead in Washington. This is primarily due to the difficulty of distinguishing natural and hatchery-origin spawners on the redds, but also reflects the challenging nature of counting redds in mid-winter. However, an understanding of the timing of spawning of natural-origin steelhead is important when evaluating potential genetic interactions with adult returns from hatchery programs. The best data set that we are aware of is for Snow Creek, a small stream that is a tributary to Discovery Bay and the Strait of Juan de Fuca. Prior to initiation of research at Snow
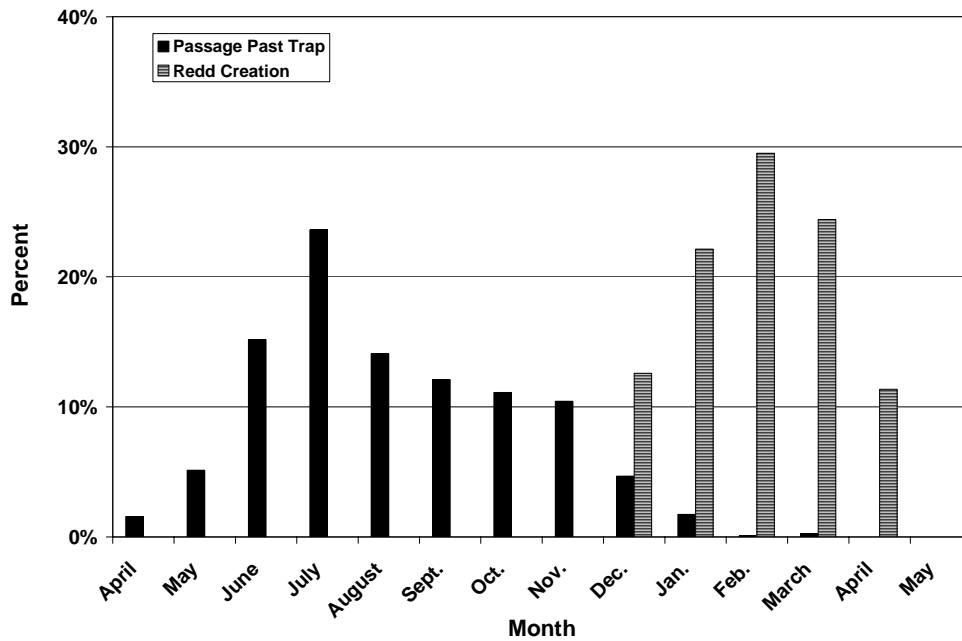
Figure 2-2. Average timing of natural-origin summer steelhead passage at the Kalama River trap (1976-1977 through 1995-1996 seasons) and redd creation (1979-1980 through 1981-1982 seasons).
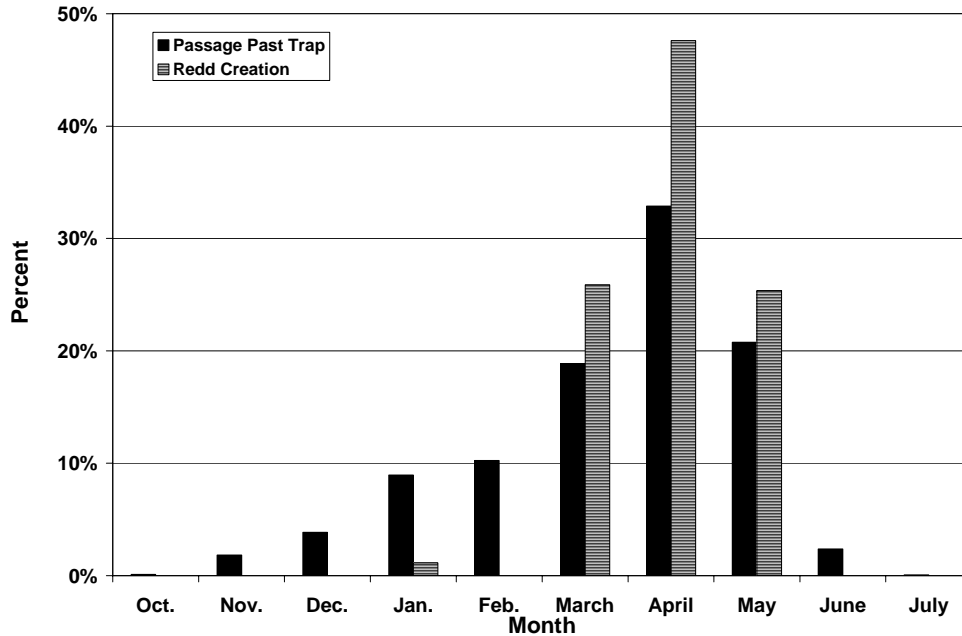

Figure 2-3. Average timing of natural-origin winter steelhead passage at the Kalama River trap (1976-1977 through 1995-1996 seasons) and redd creation (1979-1980 through 1981-1982 seasons).

Creek, no hatchery-origin smolts had been released into Snow Creek and, in the return years 1977-1978 and 1979-1980, any hatchery-origin strays from other watersheds were identified as they were passed upstream at a rack (Johnson et al. 1978; Johnson et al. 1980). Based on analysis of scale patterns, only one hatchery-origin steelhead is known to have been passed upstream during these two years. Redd surveys were conducted at approximately one week intervals with redds first observed on February 4 (1980) and the last new redds constructed were observed on May 24 (1978). Over the two years, the average date of redd construction was March 28 with a standard deviations of 18.1 days (Fig. 2-4).
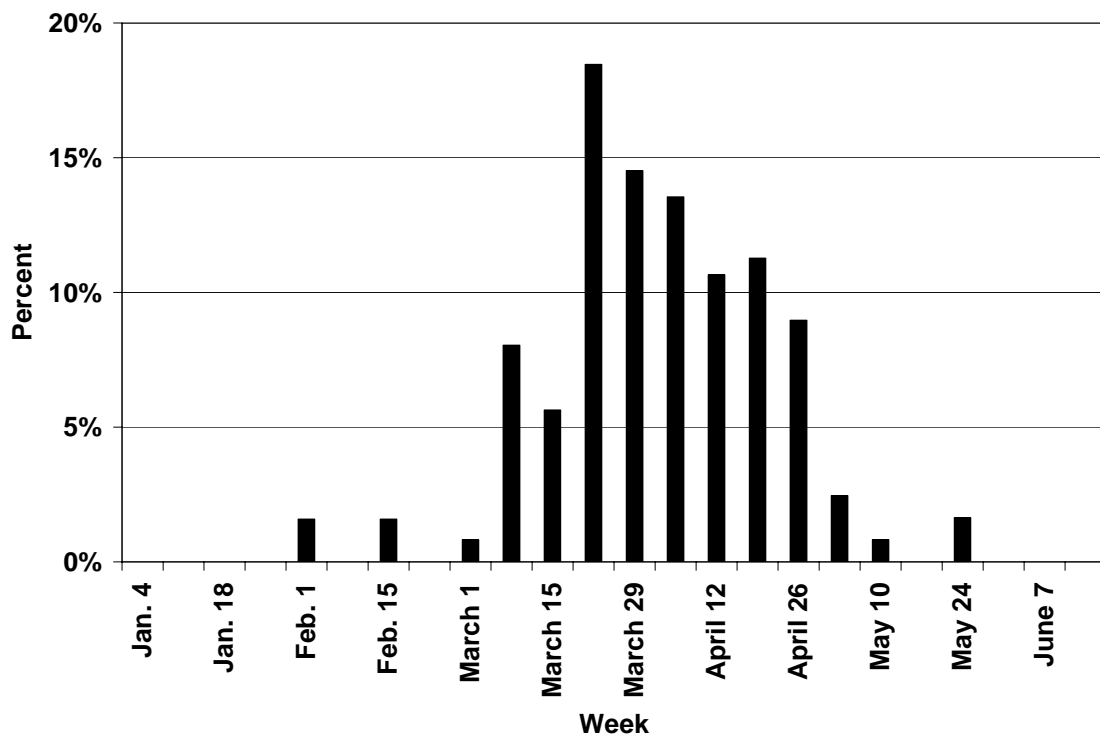

Figure 2-4. Average percent of total redds constructed by week for natural-origin winter steelhead in Snow Creek, 1977-1978 and 1979-1980 seasons.

More limited information on the spawn timing of winter steelhead is available for the Clearwater River, a tributary to the Queets River on the north Washington coast. Redd surveys were conducted in the mainstem of the Queets River and in tributaries on an irregular schedule in the years 1973 through 1980 (Cederholm 1984). Cederholm reported survey data for every year from 1973 through 1980, but 1978 was the only year with at least one survey in each of the months of January, February, and March. As in Snow Creek, no releases of hatchery-origin steelhead had occurred in the watershed in

the years prior to the surveys. However, unlike Snow Creek, the incidence of hatchery-origin steelhead that may have strayed from other watersheds is not known. Cederholm found that redd construction appeared to occur earlier in the tributary streams than in the mainstem Clearwater River. The average date that a new redd was seen in the tributaries was March 27 versus April 21 in the mainstem of the Clearwater River (Table 2-1).

Table 2-1. Average date and standard deviation for observations of new redds for winter steelhead.

Location	Average date new redd observed	SD (days)	Years	Source
Snow Creek	March 28	18.1	1977-1978 1979-1980	Johnson et al. (1978); Johnson et al. (1980)
Clearwater River Tributaries	March 27	35.9	1977-1978	Cederholm (1984)
Clearwater River	April 21	20.4	1977-1978	Cederholm (1984)
Kalama River	April 12	23.1	1979-1980; 1980-1981; 1981-1982	Leider et al. (1984)

Significant complexity is introduced in fishery management and monitoring in watersheds with populations of both summer and winter steelhead. When developing fishing regulations, the abundance, spatial distribution, and run timing of summer and winter steelhead must be considered. Catch and escapement data must be collected, maintained, and analyzed separately for each run-timing component to accurately evaluate population productivity and status. Monitoring the smolt production from the adults of each run timing within a watershed may not be feasible because no visible differences exists between juvenile summer and winter steelhead. Although summer and winter run steelhead are generally quite similar genetically, new methods of DNA analysis may be able to distinguish smolts of each type. However, this would likely entail a substantial investment of staff time to sample the smolts and analyze the genetic samples.

2.4.2 Iteroparity

A species is called iteroparous if individuals can reproduce more than one time throughout their life. Steelhead and cutthroat (*Oncorhynchus clarkii*) are the only species of *Oncorhynchus* in Washington that typically display iteroparity. Male Chinook

salmon (*Oncorhynchus tshawytscha*) that breed without migrating to marine waters may also spawn multiple times under unusual conditions (Unwin et al. 1999).

Adults that return to reproduce a second time are generally females (Withler 1966; Ward and Slaney 1988) that have been in marine waters for as little as 2-6 months but more typically one year. These repeat spawners can comprise a significant proportion of the run; up to 23% the total spawners have been repeat spawners in the Quillayute River (Table 2-2). More typically in Washington, 5-10% of the winter run is comprised of repeat spawners. The incidence of repeat spawners among summer steelhead in the interior Columbia Basin is lower, generally 0-5% of the run (Table 2-2).

Variations in the incidence of iteroparity among populations reflect both natural and anthropogenic factors. Natural factors include both the latitude and the distance of the migration inland (Withler 1966; Busby et al. 1996; Fleming 1998). A decreasing incidence of repeat spawners is evident for populations north of Oregon and for populations with substantial migration distances inland (e.g., tributaries to the upper Columbia River and Snake River). Anthropogenic factors can directly or indirectly effect the incidence of repeat spawners. Direct effects can include an increase in the mortality of kelts (e.g., Evans and Beaty (2001) describe dam passage mortality) or fishery related reductions in the number of spawning adults. Larson and Ward (1954), for example, suggest that the "larger percentage of re-spawners entering the catch in the Hoh River in 1948-49 was undoubtedly the result of the long periods of high water during the 1947-48 season, when flood conditions caused the sport catch and the Indian catch to drop to a low level." Anthropogenic factors may also indirectly affect the incidence of repeat spawners by changing the intensity of density-dependent processes, growth rates, or other processes that ultimately affect the age structure and maturation rates of the population (Fleming 1998).

The limited historical information available does not indicate that a change in the incidence of repeat spawners has occurred since at least the late 1940s. Larson and Ward (1954) compiled age data for winter steelhead from four rivers (Green, Hoh, Chehalis, and Cowlitz) and found that repeat spawners comprised an average of 6-10% of the run.

Iteroparity can significantly complicate analyses that attempt to define a relationship between the number of spawners and abundance in the subsequent generation. Traditional stock-recruit analyses, such as the Beverton-Holt or Ricker model, assume that all fish die after spawning. Although extensive mathematical theory and models have been developed for iteroparous species (see Quinn and Deriso 1999), these have rarely been applied to steelhead. If large variations in the frequency of repeat spawners occur, abundance forecasts that rely on the average frequency may have significant error.

2.4.3 Variable Length of Freshwater and Marine Residence

Steelhead can spend from 1-7 years in freshwater and 0-5 years in marine waters before returning to spawn (see Box 2-1 for a description of the methods used to determine the age of steelhead). However, the majority of winter steelhead in Washington smolt after two winters in freshwater and subsequently spend one winter in marine waters (age 2.1+)(Table 2-3). While that same life history pattern is seen for summer steelhead, the primary age class for summer steelhead in the Kalama, Yakima, and Wenatchee rivers spends two full winters in marine waters (age 2.2).

Estimating the age composition of the adult return can be difficult if a random sample of adults from throughout the run cannot be collected. Age and sex composition can vary during the return, and fishing can be size and age selective. In the Quillayute River, for example, winter steelhead that were in marine waters for two winters appear to return to the river prior to adults that spent just one winter in marine waters (Fig. 2-5). In the 12 return years of 1981-1982 through 1992-1993, the ratio of age 2.1+ to age 2.2+ adults in the sport catch averaged 0.7 in November and 2.6 in April. The percentage of repeat spawners in the sport fishery catch also increased during the season, averaging 1-2% in November and December but 8-9% in February and March (Fig. 2-6). Shapovalov and Taft (1954) also found that repeat spawners comprised a larger percentage of the latter part of the run in Waddell Creek, California.

Although providing a hedge against environmental variability, the multiplicity of freshwater and marine ages can make it difficult to estimate the productivity of a population. Since the production resulting from a single brood year can return over a period of many years, accurate estimates of productivity require that the age composition of the run be estimated in each year. Obtaining a random sample of adult steelhead can be difficult. Fishing gear is often size-selective and, because steelhead do not die immediately after spawning, finding spawned-out carcasses to sample for scales is rarely feasible. If large variations in age structure occur, abundance forecasts that rely on the average age at return may have significant error.

Table 2-2. Percentage of repeat spawners observed for natural-origin summer and winter steelhead at select locations Washington.

Watershed & Run	Geographic Location	Average % repeat spawners (range)	Source (years)
Summer Steelhead			
Kalama	Lower Columbia	7% (3-15%)	Hulett (pers. comm.) (1975-1976 through 1997-1998)
Touchet	Middle Columbia	4% (0-8%)	Bumgarner et al. (2004) (1993-1994 through 2004-2005)
Yakima	Middle Columbia	3%	Hockersmith et al. (1995) (1989-1990 through 1992-1993)
Wenatchee	Upper Columbia	0% (0-0%)	Murdoch (pers. comm.) (1997-1998 through 2004-2005)
Methow & Okanogan	Upper Columbia	1% (0-3%)	Murdoch (pers. comm.) (1997-1998 through 2004-2005)
Tucannon	Snake	1% (0-3%)	Bumgarner et al. (2004) (1999-2000 through 2004-2005)
Winter Steelhead			
Skagit	Puget Sound	6% (0-14%)	Bernard (pers. comm.) (1985-1986 through 2004-2005)
Snohomish	Puget Sound	9% (0-18%)	WDFW unpublished data (1980-1981 through 1991-1992)
Green	Puget Sound	6% (5-7%)	Meigs and Pautzke (1941) (1939-1940 through (1940-1941)
Green	Puget Sound	6% (0-19%)	Cropp (pers. comm.) (1977-1978 through 2004-2005)
Snow Creek	Puget Sound	9% (0-33%)	Johnson (pers. comm.) (1976-1977 through 2004-2005)
Hoh	Olympic Peninsula	10% (7-14%)	Larson and Ward (1954) (1948-1949 through 1949-1950)
Quillayute	Olympic Peninsula	11% (4-21%)	Cooper (pers. comm.) (1978-1979 through 2004-2005)
Chehalis	Washington Coast	9%	Larson and Ward (1954) (1947-1948)
Cowlitz	Lower Columbia	6% (4-8%)	Larson and Ward (1954) (1946-1947 through 1947-1948)
Kalama	Lower Columbia	9% (4-20%)	Hulett (pers. comm.) (1975-1976 through 1997-1998)

Table 2-3. Primary age classes of natural-origin summer and winter steelhead in Washington. % is average percentage of adult return comprised of that life history pattern.
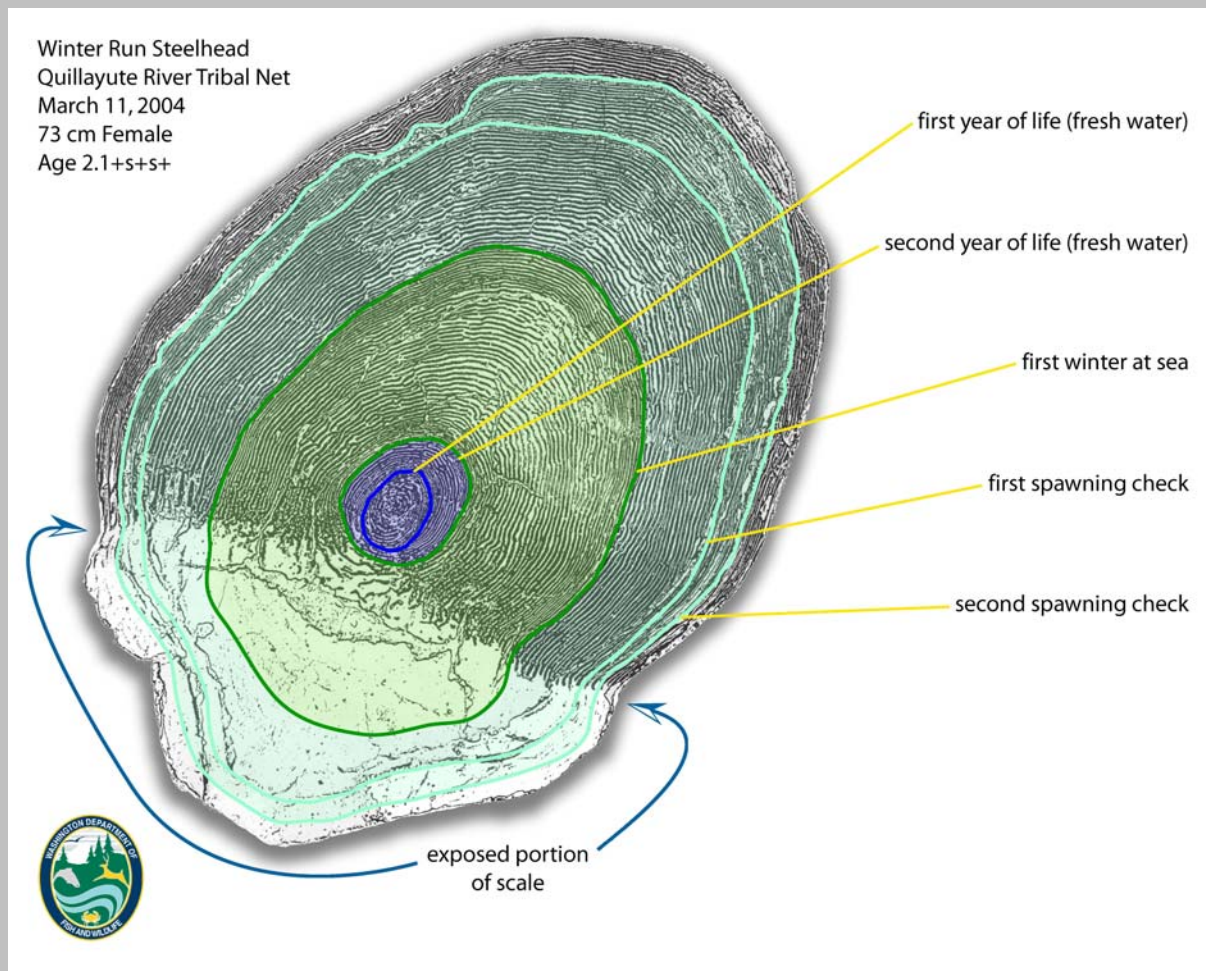
Watershed (sampling method)	Geographic location	Life history patterns		Source (years)
		Primary (%)	Secondary (%)	
Summer Steelhead				
Kalama (weir)	Lower Columbia	2.2 (61%)	2.1 (12%)	Hulett (pers. comm.) (1975-1976 through 1997-1998)
Yakima (weir)	Middle Columbia	2.2 (43%)	2.1 (26%)	Hockersmith et al. (1995) (1989-1990 through 1992-1993)
Touchet (weir)	Middle Columbia	2.1 (40%)	2.2 (35%)	Bumgarner et al. (2004) (1993-1994 through 2004-2005)
Wenatchee (weir)	Upper Columbia	2.2 (38%)	2.1 (30%)	Murdoch (pers. comm.) (1997-1998 through 2004-2005)
Methow & Okanogan (weir)	Upper Columbia	2.1 (42%)	2.2 (39%)	Murdoch (pers. comm.) (1997-1998 through 2004-2005)
Tucannon (weir)	Snake	2.1 (43%)	2.2 (31%)	Bumgarner et al. (2004) (1999-2000 through 2004-2005)
Winter Steelhead				
Skagit (sport catch)	Puget Sound	2.1+ (44%)	2.2+ (26%)	WDFW unpublished data[1] (1978-1979 through 1992-1993)
Green (sport catch)	Puget Sound	2.1+ (52%)	2.2+ (13%)	Meigs and Pautzke (1941) (1939-1940 through 1940-1941)
Green (sport catch)	Puget Sound	2.1+ (45%)	2.2+ (38%)	Cropp (pers. comm.)[2] (1977-1978 through 1989-1990)
Snow Creek (weir)	Puget Sound	2.1+ (66%)	2.2+ (9%)	Johnson (pers. comm.) (1976-1977 through 2004-2005)
Hoh (sport catch)	Olympic Peninsula	2.1+ (75%)	2.2+ (14%)	Larson and Ward (1954) (1948-1949 through 1949-1950)
Quillayute (sport catch)	Olympic Peninsula	2.1+ (48%)	2.2+ (33%)	WDFW unpublished data (1979-1980 through 1992-1993)
Chehalis (sport catch)	Washington Coast	2.1+ (66%)	2.2+ (15%)	Larson and Ward (1954) (1947-1948)
Cowlitz (sport catch)	Lower Columbia	2.1+ (58%)	2.2+ (22%)	Larson and Ward (1954) (1946-1947 through 1947-1948)
Kalama (weir)	Lower Columbia	2.1+ (51%)	2.2+ (28%)	Hulett (pers. comm.) (1976-1977 through 1998-1999)

[1] 1982-1983, 1983-1984, and 1991-1992 seasons excluded because fishery closed prior to the end of March.

[2] 1983-1984 and 1984-1985 seasons excluded because fishery closed prior to the end of March.

Box 2-1. Ageing Steelhead

The age of a steelhead is often determined from the pattern of rings, or circuli, observed on a scale (see picture below). The circuli are laid down on the scale as the fish grows, with closely spaced circuli corresponding to periods of slow growth. During the winter, the prolonged period of reduced growth results in an area on the scale, termed the annulus, with a substantial number of closely spaced circuli. Counting the number of annuli provides a means to determine the age of the fish from which the scale was removed. The return and residence of adults in freshwater results in a loss of body mass and resorption of the edge of the scale. The number of times a fish has previously returned to freshwater can be determined from the number of areas of resorption.

Winter Run Steelhead
Quillayute River Tribal Net
March 11, 2004
73 cm Female
Age 2.1+s+s+

first year of life (fresh water)

second year of life (fresh water)

first winter at sea

first spawning check

second spawning check

exposed portion
of scale

Box 2-1. Ageing Steelhead (continued)

The Washington Department of Fish and Wildlife uses a modified version of the Narver and Withler (1971) scale aging method to age steelhead scales. This ageing method for steelhead consists of chronological arrangements of the following symbols:

"." = initial saltwater entry.

Arabic numerals = number of consecutive winters in freshwater or in saltwater. To qualify for a numeral the annulus must be followed by more widely spaced circuli (i.e.: spring or summer growth).

"+" = used for winter-run steelhead only, indicates less than one year in salt or freshwater, usually denotes spring and/or summer circuli but may include some winter circuli (after a period (".") a "+" denotes saltwater existence).

"S" = spawning check, represents approximately 1 to 6 months for winter-run fish or 6 to 12 months for summer-run fish.

"+S" = one chronological year for winter-run steelhead.

"W" = Wild designation, used to identify natural-origin steelhead that smolted and entered saltwater after one year in freshwater.

Combinations of freshwater age, total age, and the corresponding WDFW age designation for winter steelhead are illustrated in the table below.

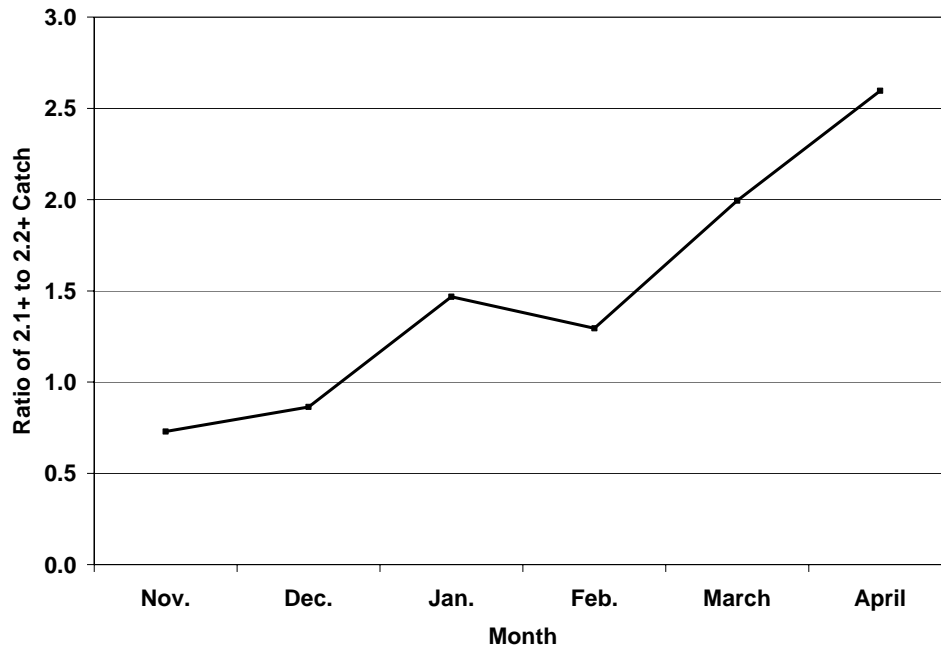| Freshwater winter(s)	Total age (years)				
	2	3	4	5	6
1	W1.+	W1.1+	W1.2+	W1.3+	
			W1.1+S+	W1.1+S+S+	W1.1+S+S+S+
				W1.2+S+	W1.2+S+S+
2		2.+	2.1+	2.2+	2.3+
			2.+S+	2.+S+S+	2.+S+S+S+
				2.1+S+	2.1+S+S+
					2.2+S+

Figure 2-5. Average ratio of age 2.1+ to age 2.2+ natural-origin winter steelhead in the Quillayute River sport fishery, 1981-1982 through 1992-1993 seasons.
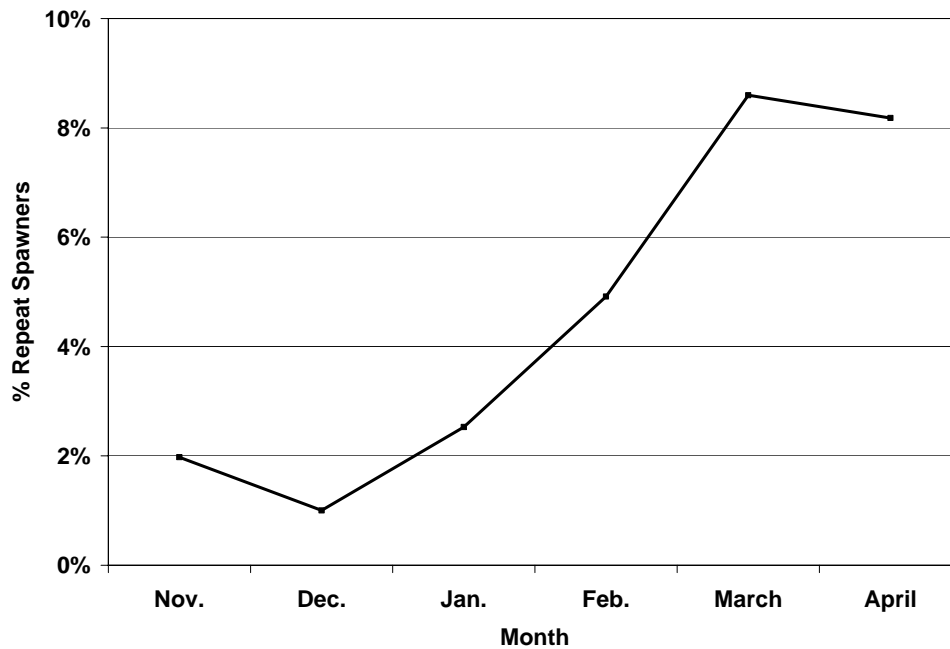

Figure 2-6. Average percentage of the Quillayute River sport catch of natural-origin winter steelhead comprised of repeat spawners, 1981-1992 through 1992-1993 seasons.

2.5 Discussion

O. mykiss displays a wide range of life history diversity that enables the species to persist in highly variable environments. The diversity of life history characteristics expressed by *O. mykiss* include the potential presence of resident and anadromous forms, varying periods of freshwater and ocean residency, summer and winter adult return timing to freshwater, and plasticity of life history between generations. The emphasis on life history diversity as a strategy for persistence contrasts with some other species of anadromous *Oncorhynchus*, such as pink salmon, that exhibit relatively small variation in life history characteristics.

Our review of the biological characteristics of *O. mykiss* suggests that maintenance of diversity, or increasing diversity where losses have occurred, should be a key consideration in the development of management plans. As the population of Washington State expands, and the potential for habitat degradation increases, this diversity provides O. mykiss with the potential to maintain viable populations. Broad-scale modifications of habitat, such as might result from global warming, further reinforce the importance of maintaining the diversity of *O. mykiss*. Similar considerations led the RSRP (2004) to conclude that "recovery plans for *O. mykiss* ESUs listed under the Endangered Species Act should place a high priority on the maintenance and restoration of naturally occurring life-history diversity, including the restoration of extirpated anadromous runs." The current diversity of steelhead populations in Washington, and monitoring needs, is discussed further in Chapter 6, Diversity and Spatial Structure.

Theoretical analyses and empirical data suggest that shifts in the relative abundance of the anadromous and resident life history types may occur in response to habitat or fishery perturbations. If reductions in the abundance of steelhead are partially or completely compensated for by an increase in the abundance of rainbow trout, assessments that evaluate trends in the abundance of steelhead, without consideration of the resident life history type, may not accurately portray the status of *O. mykiss*. The population viability analyses presented in Chapter 7 (Abundance and Productivity), for example, relies only on the escapement of steelhead. Estimates of extinction risk resulting from this analysis are likely to have a positive bias for populations comprised of both steelhead and rainbow trout.

2.6 Findings and Recommendations

Finding 2-1. *O. mykiss* **displays a wide range of life history diversity that enables the species to persist in highly variable environments.** The diversity of life history characteristics expressed by *O. mykiss* include the presence of resident (rainbow or redband trout) and anadromous (steelhead) forms , varying periods of freshwater and ocean residency, summer and winter adult return timing to freshwater, and plasticity of life history between generations. The emphasis on life history diversity as a strategy for persistence contrasts with some other species of anadromous *Oncorhynchus*, such as pink salmon (*Oncorhynchus gorbuscha*), which exhibit relatively small variation in life history characteristics.

>*Recommendation 2-1.* Pursue opportunities to preserve and restore population structure, spatial structure, and within-population diversity through careful review of harvest, hatchery, and habitat management and implementation of improved strategies.

>*Recommendation 2-2.* Develop improved tools that relate environmental factors (e.g., climate, water temperature, stream flow) and the physiological status (e.g., length, growth rate) of juvenile *O. mykiss* to the diversity, spatial structure, abundance, and productivity of steelhead populations.

Finding 2-2. **The diverse life histories of steelhead introduce management complexity.** Juvenile *O. mykiss* observed in freshwater may have originated from resident or anadromous parents, and anadromous parents may be of summer or winter return-timing. This diversity can make the collection and interpretation of juvenile genetic or abundance data difficult.

The adult run of steelhead may be comprised of fish with multiple return-timing (summer and winter), a variable number of years of freshwater and marine residence, and adults that previously spawned. Understanding the effects of the environment and the number of spawners on the dynamics of the population requires age and run-timing specific estimates of fishing mortality and escapement. In some populations, further management complexity may be introduced by the contribution of resident *O. mykiss* to the production of steelhead.

Finding 2-3. **The complex reproductive and ecological interactions between anadromous and resident forms of O. mykiss may necessitate a holistic assessment of management actions.** Initial research suggests that extensive reproductive and ecological interactions can exist between resident and anadromous *O. mykiss* in some watersheds. These interactions can include breeding between resident and anadromous forms and the production of anadromous progeny from one or more resident parents.

Where substantial interactions occur, predicting or understanding the response of the population to management actions will require a holistic assessment of resident and anadromous *O. mykiss*.

> *Recommendation 2-3.* Build on studies in the Cedar River, Yakima River, and other locations to develop a better understanding of the relationship of resident and anadromous *O. mykiss*. From these studies, develop improved tools to assess the potential effects of management actions and enhanced management strategies that effectively address resident and anadromous life history forms.

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